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STUDIES OF GASTROPODA

III. ON ORTHOGENETIC VARIATION IN GASTROPODA¹

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ORTHOGENETIC variation may be defined as progressive variation along definite or determinate lines, whether such variation is along the line of increasing or decreasing complexity; i. e., aggradational or degradational. In the first place orthogenetic variation is *ontogenetic*; i. e., the successive changes which the individual undergoes in its transformation from embryo to adult follow each other in definite succession, the changes appearing step by step. When we are convinced that the changes seen in the development of the individual are reminiscent of the changes passed through by its successive ancestors, it becomes apparent that *phylogenetic* variation is also orthogenetic, or along definitely determinable lines.

It has been the general custom to test the validity of the recapitulation theory by the embryological method; i. e., the comparableness of the changes which the individual undergoes during its embryonic period, to the adults of more primitive types. Usually the comparison has been with adults of existing types, since in most cases these alone were available for comparison. It is no wonder, then, that such comparisons have led to innumerable errors, if not absurdities, which have placed the recapitulation

¹ The previous numbers of these "studies" appeared in the *American Naturalist* as follows: No. I, vol. XXXVI, no. 432, pp. 917-945, Dec. 1902; No. II, *Fulgur* and *Sycotypus*, vol. XXXVII, no. 440, pp. 515-539, Aug. 1903.

² Investigations carried on by the aid of a grant from the Hermann Fund of the council of the Scientific Alliance of the city of New York.

theory in an evil light, and awakened in the minds of many serious investigators doubts as to the validity of the deductions based upon this doctrine. When, however, the entire life history of the individual is considered, instead of only the embryonic period, and when the successive stages of epembryonic development are compared with the adult characters of related types in immediately preceding geologic periods, it will be found that the fundamental principle of recapitulation is sound, and that the individuals do repeat in their own epembryonic development the characters of their immediate ancestors.

One of the great mistakes made by the majority of systematists is the disregard of the immature stages of development; i. e., the stages between the embryonic and adult. This is notably the case among writers on recent mollusks, who either ignore the early stages entirely in their specific description or give them the briefest notice. And yet it is in these early stages that we find the key to the affinities of a given species with others of its kind, in the present and in past faunas, more often and more surely than in the adult characters. To classify by adult characters only is to neglect the nearest and most obvious method for the ascertainment of the line of descent of the species in question; and, further, it is to leave out of consideration the inevitable similarity produced in the aspect of adult types of different origins, by a loss of the characters distinctive of their respective ancestors and of their younger stages. The classification into one family of all bald headed men of the same age would not be more illogical than some of the classifications of phylogerontic mollusks in vogue today,—classifications based wholly on adult characters. Agassiz long ago called attention to the need of considering the stages between the embryo and adult, as the following extracts will show.

“Embryologists have generally considered their work as completed when they have traced the new being to a point at which it resembles somewhat any of the members of the natural group to which it belongs. The process by which the gradual completion of the whole frame is attained has been assumed to be of little interest, hardly deserving the careful scrutiny of the embryologist; while the zoologist has also overlooked, or regarded as of little importance, the differences which still distinguish the young from

the adult, even after its typical characters are perfectly distinct.”¹ And again: “. . . I would say to all young students of Embryology that their next aim should be to study those intermediate phases in the life of a young animal, when, having already acquired independent existence, it has not yet reached the condition of the adult. Here lies an inexhaustible mine of valuable information unappreciated, from which. . . may be gathered the evidence for the solution of the most perplexing problems of our science.”²

AVAILABILITY OF THE MOLLUSCA FOR THE STUDY OF DEVELOPMENTAL STAGES

Of all classes of organisms, the mollusks are perhaps the best adapted for the study of ontogenetic stages between the embryo and the adult, since all these stages are preserved as a permanent record in the form of the shell. Such a record cannot, of course, be obtained from the soft parts, where a number of individuals are necessary to represent the principal stages. Moreover, a certain step in development may be very definitely indicated in the form and sculpture of the shell, and yet be entirely unrecognizable in the soft parts. Not only, then, is the shell a permanent record of the changes, but it is also a more delicate register of advancement than is afforded by the soft parts. In other groups of organisms, the record is seldom so complete, though brachiopods and corals retain, in perfect specimens, all the earlier stages. Other organisms, however, such as the echinoderms and vertebrates, preserve in their hard parts only the record of the stage at which the animals die, since these hard parts undergo individually constant changes from youth to maturity.

Among the mollusks, the gastropods and cephalopods are the most satisfactory for ontogenetic investigations, since in them the early stages are not only well preserved, but there are also a large number of characters the progressive variations of which may be studied. In many respects gastropod shells are the simpler to study, because the greater parts of the whorls are freely exposed

¹ Agassiz, *Methods of Study in Natural History*, Chapter XVI.

² *Ibid.*, Chapter XV.

and open to observation, whereas in the coiled cephalopod shells the outer whorls must be removed before a satisfactory view of the inner ones can be obtained. Despite this fact, the study of shell ontogeny has been mostly confined to the cephalopods, especially to the highly complex and often richly ornamented ammonite shells; and this can hardly be wondered at, when we consider their number, and the high degree of diversity found in this group of organisms.

ORTHOGENESIS IN THE ONTOGENETIC DEVELOPMENT OF GASTROPODS

The individual development of gastropod shells always follows one of a small number of lines of variation. Leaving aside color markings, which have been somewhat fully discussed by the Countess von Linden,¹ we may devote this discussion to the changes in form and ornamentation. At the outset, however, we must note that in every perfect shell there are two parts to consider; namely, the protoconch and the conch. These may be continuous with each other, in which case the features of the protoconch merge into those of the conch; or they may be discontinuous, when the protoconch features end abruptly and the conch features begin as abruptly. (See *Studies of Gastropoda*, I, fig 5.)

The form of the gastropod shell is manifold, but the types are few. Primitive types always begin with rounded whorls free from all ornamentation. The coiling of the whorls at first is in a sufficiently loose manner to produce a hollow axis, opening below in an umbilicus. Even in types in which the anterior end of the adult is produced into a canal — as in *Fulgur*, *Buccinum*, *Fasciolaria*, etc.— the earliest protoconch stage has been found to show the umbilicated round-whorled condition (*Studies of Gastropoda* I, fig. 3). This condition may be accompanied by various modifications in the amount of embracing of the succeeding whorls. In all cases a moderate amount of embracing by the succeeding whorls seems to be the simplest condition, although it must be borne

¹ Die Entwicklung der Skulptur und der Zeichnung bei den Gehäuse-schnecken des Meeres. *Zeitschr. f. wissenschaft. Zoologie*, LXI, p. 261.

in mind that a difference may here be found between protoconch and conch. When the whorls embrace but slightly, a deep suture is produced between them. In this case the spire also is a slender one, as is shown in so many primitive fusoid shells (Studies I, fig. 6). As the amount of embracing increases, the suture becomes less strongly depressed, and the spire takes on an ever greater apical angle. The amount of embracing may increase until the suture is found at the ambitus of the preceding whorl (Studies II, fig. 13). Beyond this, the embracing is only carried in the old age of the individual of normal types or in specialized types, generally the members of a phylogerontic series.¹

In a large number of types, the amount of embracing by the whorl remains practically the same throughout life, thus giving the spire a uniform angle. In others, again, and perhaps in the majority of specialized types, the embracing is at first less, but slowly increases in amount with each succeeding whorl in the later stages (Fig. 1).

Even in degradational types, where the embracing of the adult shell is in extreme excess of that of the normal adult type, the amount of embracing increases regularly from its first appearance to the completion of the growth.

There is another extreme found in phylogerontic members of a certain group of Gastropoda and so far observed in the non-canaliculate types only; namely, the loss of the power to coil, due to the equalization of the rate of increase in all portions of the shell (Studies I, figs. 14 and 15). This results in a looser coiling or complete straightness of the final portion of the last whorl, and may or may not be accomplished by an increase in the diameter of the whorl. Ontogenetically this is often expressed by a progressive loosening of the coil, though there are various degrees of abruptness, some coils becoming gradually straightened, while in other types this straightening appears very abruptly. As will be shown presently, the loss of power to coil and the excessive spread-

¹ The nomenclature of stages in development, devised by Hyatt, Buchmann, Bather and others, is for ontogenetic stages as follows: *nepionic*, babyhood; *néanic*, youthful or adolescent; *ephebic*, adult; *gerontic*, old age or senile. Corresponding stages in phylogenesis are designated by the prefix *phylo*, but the term *phylogerontic*, or racial old age, is the only one in common use.

ing of the whorl are generally accompanied by the loss, or at least a modification, of the ornamentation.

A second important type of modification of form in ontogeny is the angulation of the whorls. This begins as a slight depression in the curvature of the upper or shoulder portion of the whorl, and a similar depression of the lower or body portion. Thus a faint angulation appears in the ambital portion of the whorl, which usually occurs where the whorl is marked by the first or most pronounced of the spirals. From a faint beginning, the angle increases in sharpness, and the depression of the shoulder surface and body surface increases, until the whorl consists of two perfectly flat or even slightly concave surfaces separated by a sharp angle (Fig. 2). Where the angulation appears late in the ontogeny, generally about an equal flat space is shown above and below the angle (Fig. 8). When it appears early, the later whorls generally embrace the preceding more strongly, thus decreasing the space below the angle, until in extreme cases this lower space has entirely disappeared, the suture of the succeeding whorl being at the angle (compare Fig. 5 with the younger portion of another individual enlarged in Fig. 2). This produces a continuous slope of the spire, which may vary, in different types, from nearly horizontal as in *Conus*, where the shoulder makes a right angle with the axis of coiling of the shell, to nearly vertical as in some *Turritellas* and *Cerithium*, where the shoulder makes a very acute angle with the axis of coiling, and the ambital angulation is far down on the shell. In all such cases, however, it is the rule that the earlier whorls are less closely coiled, so that in the young spire the flattened body of the whorl, below the angulation, becomes visible (Fig. 2). This is true even of such highly specialized types as *Conus*, where the shoulders alone of all the later whorls are visible; for the young whorls here project commonly above the general surface, showing a more steeply sloping shoulder, and generally exhibiting a portion of the whorl below the angulation, though this portion may be the merest fraction of the whorl. Rarely has acceleration gone so far that the shell begins with an angle and the whorls embrace up to the angle. The norm of the embracing, as in the slope of the shoulder, seems to be that which approaches most nearly to the round-whorled condition; i. e., an equal exhibition of flattened

shoulder and body, and approximately an angle of 45° between the shoulder and the axis of coiling. From this the progressive change is to a steeper shoulder in one series and to a flatter shoulder in the other. Similarly, the partial embrace of the whorls seems to be the norm, from which variation on one hand is in the direction of more pronounced embracing, carried to excess in phylogerontic

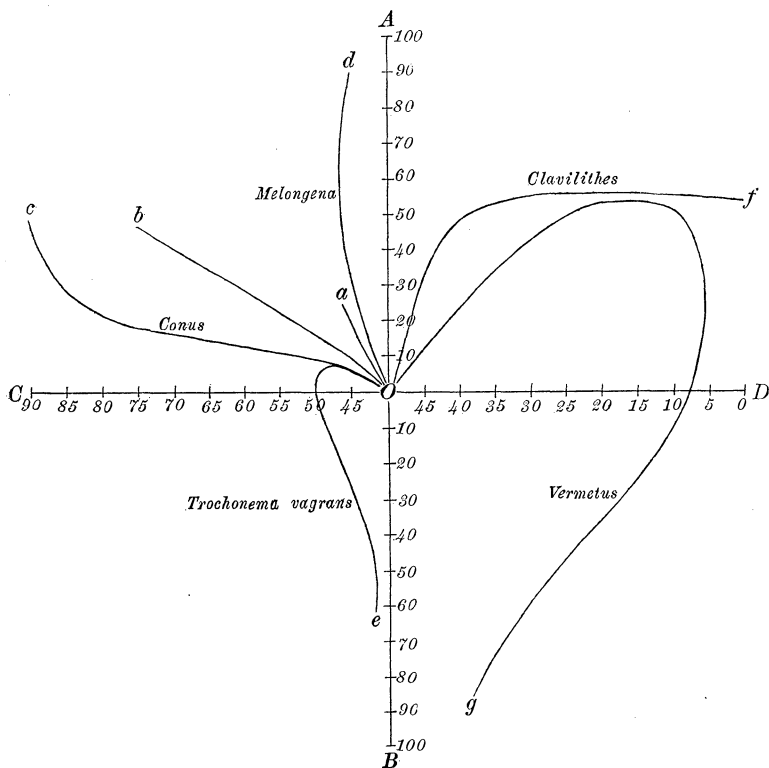


Diagram 1.—To illustrate the development of various types of gastropod shells, as explained in the text.

types, and in the other to a gradual loss of power to coil, which also terminates in a phylogerontic condition. These relationships may be represented in the following manner (Diagram 1).

The ambitus of the whorl, or the point of greatest convexity, is taken as the center of the whorl. The line $O - A$ represents progressive increase in embracing, from zero at O to 50% at the ambitus, and to complete overlapping and concealing of the pre-

ceding whorl at A (100%). $O - B$ represents progressive loss of coiling power to straight conditions at B ; $O - C$, increasing horizontality of shoulder from round at O to 45° and thence to horizontal or 90° with reference to the axis of coiling. $O - D$ in the same way represents increasing verticality from 45° to 0° , or parallelism with reference to the axis of coiling, at D .

A simple round whorled shell in which the whorls do not embrace throughout life (primitive *Fusus*) would be represented by the point O . One in which a slight amount of embracing occurs, but no change in outline of whorl, is represented by a line on $O - A$, the length of which marks the percentage of embracing up to 50 at the ambitus or more if the whorls overlap. The line may not start at O but higher up, the earlier whorls showing some embracing. The line $O - a$ represents the life of a shell in which the whorls gradually change to angular (45°) and the embracing increases up to 25% or half way to the ambitus.

$O - b$ represents a shell with gradual increase of embracing of whorls to ambitus, and flattening to 75° with reference to the axis of coiling, as in some *Fulgurs*. $O - c$ represents a more rapid flattening than increase in embracing, as in *Conus*; $O - d$ a gradual increase in embracing to below the ambitus, while at the same time the whorls are flattened to a shoulder of 45° . Then the embracing continues to the ambitus, beyond which, with increasing embracing, the whorls lose their angularity. This is seen in *Melongena*. In *Clavilithes*, represented by $O - f$, embracing increases to the ambitus, after which the whorls become quickly flattened vertically to 0° . *Vermetus* is represented by $O - g$, in which increasing embracing and flattening to 10° or less represents the *Turritella* stage, after which a loss of the embracing finally brings us to the loose coiling type with a return to round whorled condition. Similar changes are seen in *Trohonema vagrans* (Studies I, fig. 15) where angular embracing whorls are succeeded by loose rounded ones.

ORNAMENTATION OF THE WHORLS.

As already shown in the first of these studies (*Am. Nat.*, XXXVI, p. 930) the ornamentation of the whorl consists of ribs, spirals,

tubercular keel, and spines. Of these, so far as ascertained, the ribs generally appear first, though in a group of early gastropods in which ribs are never developed in the adult, spirals may be well developed. The point of importance, however, is not the relative time of appearance, but the mode of development of each, and their influence upon each other when they occur together. Where the development is complete, the ribs are at first faint vertical ridges upon a rounded whorl, enlarging gradually until they are strong, rounded, elevated ridges extending from suture to suture, with their greatest prominence at the ambitus of the whorl (Figs. 16-17). From being at first rather distant, they may increase in breadth until they are separated only by a depressed line. With the appearance of the ambital angulation, the ribs become fainter towards the sutures, while at the same time they become more pronounced upon the ambitus. Eventually the ribs disappear entirely from the shoulders, disappearing at the same time or somewhat later from the body of the whorl below the shoulder angle. Then only a regular row of tubercles remains behind, each tubercle being the concentrated essence of the ribs of the earlier stages (Studies II, fig. 10). Throughout, this process of metamorphosis is a regular progression, though in some (i. e., accelerated) shells it occupies a smaller number of whorls than in others. Up to this point there is uniformity in development of all ribbed shells with angular whorls following upon rounded ones. Beyond this point there is a divergence; along one line the tubercles gradually broaden and become confluent into a keel (Studies II, fig. 12) which forms a prominent and persistent character, disappearing only in old age types when the shell becomes rounded; along another line the keel, if it comes into existence quickly disappears, when the shell becomes rounded in outline. Upon this a new type of ornamentation, the spine, appears. This will be more fully discussed below.

The spirals.—These are continuous and persistent folds in the shell substance, caused by a slight emargination in the lip of the shell. This emargination corresponds to a faint wrinkle in the mantle when withdrawn, the growth of that organ being a more rapid one than is commensurate with the increase in diameter of the whorl. Thus while when expanded, the mantle is smooth,

when withdrawn it must be folded into minute wrinkles to become accommodated to the smaller space. That these spirals are generally visible only as emarginations on the margin of the lip, indicates that only the outer portion of the mantle is affected by this excess of growth. If other parts of the mantle are affected, lirae result on the inside of the outer lip and plications on the columellar lip.

The order of appearance of the spirals is a very regular and progressive one. In simple or primitive shells a single spiral makes its appearance at the ambitus, followed in most cases successively by spirals above and below. A partial exception to this rule is found in types in which a certain number of stages have been dropped out between the protoconch and conch and hence the conch does not begin at the beginning (Studies I, fig. 5) but at a stage normally belonging later in the ontogeny. Thus in *Fusus*, *Latirus*, *Semifusus* and certain *Murices* the conch begins abruptly with rounded ribs and three or more spirals. Such dropping out of early stages is however entirely in conformity with the general progress of development and is itself progressive, or orthogenetic. It belongs however in the category of phyletic orthogenesis.

At whatever stage of development the shell begins, that development is thereafter progressive. Thus in a large number of forms, if the shell begins with three spirals, the fourth, fifth and later spirals appear progressively above the upper, and below the lower one. If the whorls become asymmetrical, with continued growth, as is the case in the majority of shells where the lower (anterior) portion is either drawn out into a spindle and canal, or is flattened and depressed, the development of the spirals will be unequally distributed. Thus in shells with a spindle, three or four spirals may appear successively below, while only one appears above the ambitus.

In some cases as in *Goniobasis*, certain *Melantias* etc., the third and later spirals appear as intercalations between the first two. In this respect they resemble the secondary spirals to which indeed they may be closely allied. They however quickly reach the size and other characters of the two first spirals with which they appear to form the primary series (Figs. 13 and 18). Additional intercalated spirals with the habitat of the secondary spirals appear between them at a later period.

The manner of appearance of the spirals must be regarded as a consequence of the rate of growth of the mantle. Considering that the first two spirals are the result of the first two folds into which the mantle border is thrown on retraction, and assuming that the position of these folds is a permanent one as appears indeed to be unquestionable from the continuity and regularity of the spirals, we perceive that if the mantle border grows more rapidly above and below the original folds than between them, the new spirals will appear respectively above and below the first two. If on the other hand the mantle grows fastest between the two original folds, the corresponding spirals will diverge and new ones appear between them. This is the case in the formation of the secondary spirals in the Fusidae and other forms. The question may well be asked if these two modes of appearance of the early spirals do not represent two lines of development originating independently in various genetic series and producing end-members, which, within the same series, are indistinguishable in their adult characters. If, on the other hand, we regard intercalation as the method of appearance of secondary and later spirals, then Gonio-basis and the Melanias and other types which show intercalation after the appearance of the first two spirals, must be considered as highly specialized and accelerated types.

When the full number of primary spirals has appeared, or in accelerated shells at an earlier period, intercalated spirals appear, beginning in the broadest interspaces. In fusoid shells this intercalation begins on the spindle, where expansion is most pronounced. Secondary spirals are followed by tertiary ones, and sometimes by spirals of a higher order, all being intercalations between the primary ones. The first spiral generally marks the point at which the ambital angulation occurs. A strengthening of this spiral is, indeed, often the first indication of approaching angularity, and in some cases the change of whorl does not progress beyond this point. When the central spiral continues to increase in size, after the ribs have been reduced to nodules, the form of these nodules will be influenced by the spiral, so that instead of knobs they will be elongated, rounded, and flattened nodes. Such a condition is well shown in *Fusus distans*. This condition often ends in complete confluence and the formation of a keel (*Sycotypus canaliculatus*).

Spines.— These are of two kinds in gastropods. In a number of phylogerontic platyceroids they consist of tubular prolongations from the surface of the shell at irregular intervals, and appear to be of little phyletic significance. The other, more important type represents a periodic emargination in the lip of the shell (Figs. 3-4, 7-8). That the periodicity of this spine formation is connected with the regular recurrence of the reproductive period, may be assumed for types in which these spines appear late in the ontogeny; but not for those in which they appear early. Direct observations in this field seem to be wanting, however. The rate of growth of the shell during the interval between such periods of spine formation determines the number of spines upon a volution. As has been shown for *Fulgur* (Studies II, p. 534) the number of periods in progressive types decreases as the shell increases in size, thus showing that the amount of growth between resting stages (i. e., spine forming stages) increases at a rate faster than the rate of increase in the size of the shell. This may of course also be interpreted as a lengthening of the time interval between resting stages, or possibly between the reproductive periods. In some forms the decrease in the number of spine periods to the whorl is a rapid one, as in *Fulgur eliceans*, where it is 12, 9, and 6 respectively for the 5th, 6th, and 7th whorl, whereas the decrease is 14, 13, 12, or 13, 12, 11 for the same whorls in *F. carica*. In *Murex (Rhino-canthus) brandaris*, on the other hand, it is 6, 6, and 7 for the 5th, 6th and 7th whorl respectively, thus showing a shortening of the growth periods. In the majority of Murices, however, the number of periods has been reduced to three for all whorls. In *Ranella* the number of resting stages as expressed by the varices has been reduced to two for each whorl.

The simplest spine is that found in *Fulgur*. It has been quite fully described in a preceding number of these "Studies" (II) and the only point that needs to be emphasized in this connection is the gradual appearance of the spine in the ontogeny of the individual. This is not noticeable in *Fulgur carica* or other accelerated types of *Fulgur*, as fully discussed in the papers referred to, but is well shown in the more primitive Miocene types (e. g., *F. tritonis*, fig. 7). Here the spines appear on a faintly keeled or smooth shell, and at first are in the form of the merest faint spinelet, scarcely

noticeable, though recognizable to the touch as a faint protuberance. From this beginning the spine grows, period by period, until it has become of the normal adult dimensions. In some forms the spine continues to grow throughout life, giving us the enormous spines of *Fulgur candelabrum*.

Where a second row of spines appears this always comes in later than the first, though acceleration may tend to shorten up the interval, or even by dropping out the earliest stages produce a type in which more than one spine appears at the beginning of the conch stage. *Tudicula* is a good example of normal succession in the appearance of spine rows. In the Miocene *T. rusticula*, only a single row of fulguroid spines appears on the ambital angulation (Fig. 3). In *T. bispinosa* sp. nov.¹ (Figs. 1, 3 and 4) the spines of the first row increase in size, progressively though slowly while a second row of spines makes its appearance lower down on the body whorl, after the first has been in existence for a considerable number of volutions. This second row begins with the merest elevation, scarcely visible though noticeable to the touch (Figs. 1 and 3). From this beginning the size of the spine increases period by period, until the spines of the second row are equal in size to those of the first (Fig. 4). In accelerated types, the second row is already well developed in the young individuals (Fig. 1).² In the modern *Tudicula spirillus*, a beginning of the second row of spines is indicated by a succession of faint elevations, each later one stronger than the preceding, but none reaching the dignity of true spines. When more than two spines occur, these follow the same rule, as may be seen in *Murex brandaris*, *M. tenuispina*, etc.

In all cases the spines appear on the spirals, representing periodic outgrowths of the emargination which originally formed the spiral. As already noted, the first spine occurs on the spiral occupying

¹ I have been unable to find that a specific or varietal name has been proposed for the forms with a double row of spines, and hence propose to use the above name for them. I am well aware that intermediate forms between those with single spinous keel and those with double spinous keel exist, but I do not consider that this militates against the specific standing of the two types.

² For a full illustration of the principal mutations of the Miocene *Tudiculas*, see Hörnes und Partsch,—Die fossilen Mollusken des Tertiär-Beckens von Wien. *Abh. d. k. k. geol. Reichsanstalt*, 1856, Bd. 3, Taf. 27.

the summit of the ambital angulation. The second row of spines generally forms on the spiral which separates the body of the whorl from the spindle. The larger spines are formed on the primary spirals, the smaller intermediate ones on the intercalated secondary and tertiary spirals. In a number of types these spines are independent (*Murex tenuispina*) while in others they become compounded. Thus in the majority of Murices, the spines of the later cycles do not become independent of those of the earlier cycles, since these earlier ones grow to such an extent that the independence of the smaller spines is impossible. Hence they become modifications upon the sides of the larger spines, and thus is produced the wonderful complexity of spine in such forms as *Murex palmarosae* and others. Here, too, as has already been shown (I, p. 934) the increase in complexity is progressive from period to period, the first formed spine on the ambitus (or shoulder angle) always leading the others. The degree of advance of the first over the second spine varies in amount in differently accelerated types; this variation is, however, phyletic and as such also progressive. In some types the second spine always has the complexity of the first spine in the preceding period, in others its complexity is comparable only with that of the primary spine in a still earlier period.

Columellar plications and lirae.—The development of these features also follows the law of progressive appearance and progressive intensification. Those types like *Fasciolaria*, *Rhopalithes*, *Latirus*, etc., which in the adult have several plications, are as a rule, free from these in the earliest stages. The only exception is in the case of accelerated types, which start conch-life already equipped with plications, as many of them start equipped with costae and spirals. In the more primitive types, however, the plications appear in succession, the first while the shell is still young, the others successively. In some cases the second plication has only reached half the size of the first in the adult shell. In types with numerous columellar plications, intercalated ones appear between the older ones. These begin chiefly in later stages of development, being absent or at least weak in the younger stages. This is well seen in the young of certain volutes, such as *Voluta musica* and *V. polyzonalis*, where the intercalated plications in

half grown shells are absent or much more weakly developed, than in the adult.

In the same way lirae appear later in the life of individuals, being absent from the earlier stages. They are furthermore often complicated by intercalations, which like the primary ones appear progressively.

SUMMARY OF APPEARANCE OF SHELL CHARACTERS.

Summarizing the results so far obtained, we note that all the characters of the shell appear in a definite order, and develop by a process of progressive intensification or growth. This law holds good in the most diverse types of gastropods as will be more fully apparent from the examples cited below as illustrations. Even where at first glance the order of development seems to be abnormal, it is seen on closer inspection that this apparent abnormality is due either to normal progressive acceleration—falling as such under the type of variation outlined in the next section, or to pathologic conditions, which cause a temporary, or sometimes permanent development of senile characters which in the normal course of the ontogeny would appear only towards the end of life.

Phyletic acceleration, or the condensation and elimination of stages normal to the ontogeny is one of the chief sources of anomalies in the ontogeny. When the elimination is at the beginning of the conch stage, the shell may be looked upon in the same light as a more primitive type in which the apical portion has been broken away. In both cases the available part begins some stages along the road of progress but in both cases the stages subsequently passed are the same, though one may go at express rate and the other at a slow pace. When however later stages are telescoped, as is the case in many accelerated forms (*Fulgur carica*, *F. eliceans*, *Fusus longicaudus*, several species of *Semifusus*, *Pugilina*, etc.) the recognition of the normal line of progress is not so easy. Nevertheless it becomes apparent that up to the point of telescoping, and from that point onward, the progress is a normal one. Merely an original detour has been cut off as a river in the course of its development cuts off a large meander, and so two points, originally far apart on the river's course are brought close together.

Many other characters of the shell, such as the outline of the spindle, and the formation of anterior and posterior canals, and the development of the color pattern, have not been touched upon, but they all proceed according to a uniform law of change. The Countess von Linden has endeavored to show that the transformation of the color pattern in marine gastropods follows Eimer's law, viz: longitudinal striping, spots, cross-stripings and uniform color.

ORTHOGENESIS IN PHYLETIC DEVELOPMENT OF GASTROPODA.

The protoconch, the last of the embryonic stages, is far less satisfactory for purposes of tracing phyletic relationship, than is the conch. Nevertheless, up to a certain point, it may, I believe, be confidently relied upon. That an early stage of the protoconch in the majority of gastropods is of the form of a simple naticoid coil with a well-marked umbilicus, has already been noted (Studies I). As stated in the first of these studies this form of the protoconch recalls the character of the earliest known coiled gastropod, i. e., *Stroparollina remota* of the lower Cambrian of the Atlantic coast province. Still earlier stages in the development of the protoconch show a capuloid form, which recalls the adult character of many of the early Cambrian shells described under various names. That all of these are not primitive but that some are phylogerontic, is shown by the fact that the earliest stages are enrolled while the later stages are non-coiling. Sardeson¹ has indeed insisted that my interpretation of such forms as *Platyceras primaevum* etc. as phylogerontic is erroneous, and he has attempted to show that the forms with slightly coiled apex are more advanced than those in which the apex is not coiled at all, and that the progress of development is from forms without any coiling through those with enrolled apex, to the close coiled types. That this is a complete inversion of the mode of coiling, must be apparent when we consider that the animal has no more power to enroll its apex, than it has to unroll it, and that, since the apical part is the first-built

¹ The Phylogenetic Stage of the Cambrian Gastropoda. *Journal of Geology*, Vol. XI, p. 470-482.

portion of the shell, it represents the primitive condition and the straightened part represents the later condition. Thus the progress of ontogenetic development is from close-coiled to non-coiled, from which we are justified in deducing that the ancestor of the type with the enrolled apex was a closely coiled type, and that the loss of power to coil, shown in the adult, is a sign of old age of the branch which that individual represents. That the earliest types were non-coiling shells cannot be doubted: there is every reason for believing that they were patelloid in form, though modern *Patella* is a phylogerontic type, which in its adult characters has returned to the condition of its forefathers. This is clearly shown by the presence of the coiled protoconch which at once stamps this form as derived from a coiled ancestor. All deductions then based on the anatomy of the soft parts of *Patella*, which leave this fact out of consideration are necessarily faulty, since it is hardly conceivable that in all its characters this animal has either remained primitive, while the shell passed through a tremendous series of metamorphoses, or that the soft parts have likewise degenerated to such an extent that they have reached in all characters the condition of the primitive ancestor of the gastropods.

Another relationship that may be deduced from the structure of the protoconch of many highly ornamented types of shells, is that they were derived from an ancestor with simple ribs on rounded whorls. Thus the ancestors of *Fusus*, certain *Murices*, *Latirus*, *Tudicula* and other types were fusoid shells with simple ribs on smooth rounded whorls, if the structure of the protoconch of these types can be regarded as an indication of ancestral conditions. For in these types the last portion of the protoconch is ribbed with delicate vertical ribs but without spirals. While the community of descent of the genera cited from some early Mesozoic ancestor is probable, it does not follow that all ribbed protoconchs indicate a common ancestry. For when it is recalled that ribs appear independently in the most divergent types of shells, it need not surprise us to find that this primitive ribbed character has been pushed back into the protoconch stage in a number of different lines of descent.

There are, of course, not wanting those who deny that the characters of the protoconch can be regarded as indicative of phyletic

relationships. Indeed the common practice of classifying largely or wholly by adult characters has almost of necessity led to a minimizing of the value of protoconchial characters when they are recognized at all. When differences of protoconch features were found in types classed together as related from adult characters it was explained as the result of the influence of different physical conditions acting upon the embryo. This heterostylism as it has been called by Boettger,¹ is explained by him as probably having one of two causes — either it is developed through a process of selection, to give the animal a lighter shell, to enable the animal occupying it to change its location more easily and quickly — or it has the object to prevent the creature from sinking into the soft ooze of the deep sea bottom, in which for lack of food or for other reasons it would perish. This of course refers only to the young shell, for the size of the initial protoconch whorl can have little significance in the adult.

Heterostylism, or a difference in the character of the protoconch in individuals living under different conditions, has been shown to exist in *Murex tribulus* L., where Sturany found that the deep sea form differs from the littoral form in an embryonic end or protoconch with more strongly swollen apical whorl, and with an extra volution. *Fusus bifrons* and *F. paucicostatus* are also distinguished at an early age by the relatively more swollen protoconch of the latter, which is at home in deeper water (490–876 meters).²

These two cases were used by Boettger³ to illustrate his heterostylism and to establish the non-validity of my contention that the character of the protoconch of *Fusus*, of *Clavilithes*, *Rhopalithes*, etc., are not only distinctive, but due to diversity of descent.⁴

¹ Boettger, O. Ueber Heterostylie bei Schneckenschalen und ihre Erklärung. *Nachrichtsblatt der deutschen Malakozoologischen Gesellschaft*; 1905, Heft 1.

² Sturany. Expeditionen S. M. Schiff Pola in das Rote Meer. *Zoologische Ergebnisse*, XXIII. Gastropoden des Roten Meeres. *Denkschr. Math. Nat. Cl. K. Akad. d. Wiss. Wien.*, 1903, Bd. 74.

³ loc. cit.

⁴ Grabau, A. W. Phylogeny of *Fusus* and its Allies. *Smithsonian Miscellaneous Collections*. Vol. XLIV, no. 1417, 1904.

A similar position with reference to my work is taken by Cossmann¹ whose criticisms are more fully considered beyond.

Referring again to the Red Sea shells cited by Sturany, and used by Boettger and by Giard² as illustrations of heterostylism in Gastropods due to diverse physical conditions, we note on reference to Sturany's illustrations that the difference between the protoconchs of *F. bifrons*, and *F. paucicosta* is one of degree and not of kind. Both protoconchs are of the same type, the true *Fusus* type; but that of *F. paucicosta* has a somewhat larger initial whorl. This species is a highly accelerated type, as compared with *F. bifrons*, and hence it is not surprising to find the protoconch partaking of this acceleration. Besides the initial larger whorl, the number of whorls appears to be less than in *F. bifrons* where $1\frac{1}{2}$ smooth volutions, followed by a delicately ribbed portion constitute the protoconch. Reference to my figures and descriptions of protoconchs of *Fusus* will show many such variations, (see pl. xvii, figs. 1-4) all of which are mere modifications due to greater or less acceleration, *but do not constitute an essentially different type of protoconch*. Such a difference of type does however exist between the protoconchs of *Fusus* and *Falsifusus* and *Fulgurofusus*, and between *Clavilithes* and *Rhopalithes* as a critical study of these will no doubt convince anyone. Where in *Fusus* of the Red Sea, the deep sea form has a larger initial and fewer subsequent whorls in the protoconch than is found in the littoral species, the deep-sea form of *Murex tribulus* combines according to Sturany a large initial with more numerous subsequent whorls when compared with the littoral type. In the absence of figures and detailed description such as one has a right to expect in a work of the kind presented by Sturany, it is impossible to judge in what this difference really consists. Moreover, one is led to doubt the accuracy of Sturany's generalizations quoted with approval by Boettger, when the statement, "It appears from these tabulations that the deep-sea examples have a proportionally higher spire, due to the increase in the number of volutions," is compared with the table

¹ Revue Critique de Palaeozoologie Oct. 1904, p. 233, and Essais de Paleconchologie comparée, liv. 7, p. 225, 1906.

² Giard, Alfred. La Poecilogenie. *Bulletin Scientifique de la France et de la Belgique*, 1905, T. XXXIX, p. 160.

of measurements to which it refers. For here we find that the smallest number of whorls (6) is found in shells from the greatest depth (920 m.) while a littoral specimen has the largest number (9) except one which has ten volutions and was obtained from a depth of 740 meters. Judging by the actual number of whorls, there appears to be nearly a steady increase in the number from 920 meters to shallow water. Moreover, it does not appear from Sturany's table how he eliminates differences in age in the individual measured. Taking shells of the same number of volutions (8) and therefore presumably of the same age, we have for

920 meters in depth — a length of 73 mm.

920 “ “ “ “ “ “ 60 $\frac{1}{2}$ “

612 “ “ “ “ “ “ 41 $\frac{1}{2}$ “

212 “ “ “ “ “ “ 57 “

Subtracting the length of the spindle we have in the same specimens the following height of spire of 8 volutions.

920 meters in depth a length of spire of 35 mm.

920 “ “ “ “ “ “ “ 27 “

612 “ “ “ “ “ “ “ 22 “

212 “ “ “ “ “ “ “ 23 $\frac{1}{2}$ “

the greatest variation being within the same depth. Since the number of volutions is here the same, this difference in height can only be ascribed to a difference of embracing in the earlier whorls. A detailed description of this difference would have been of extreme interest, and as a record of variation would have been far more valuable than the tabulation of lengths and numbers of volutions, which without further discussion are of very little significance and value.

So long as the difference of protoconchial characters lies in the somewhat larger size of the initial whorl, or the relative number of whorls, this difference may very well be regarded as due to the difference of environment. That the environment may influence the development by retarding or accelerating it, seems hardly questionable, and that as the result of such retardation or acceleration the circumferential growth of the original shell may increase proportionately more rapidly than the spiral growth, thus producing a larger initial whorl, is also comprehensible. As is shown by studies of the embryonic development of *Fulgur carica* and

Sycotypus canaliculatus the size of the initial whorl is determined by the size of the embryo long before it leaves the egg-case, and in fact the whole protoconch is formed and the animal has begun the building of the conch before it becomes free. The same thing is true of *Fasciolaria gigantea* and *Buccinum undatum* (see Studies. II, p. 535). To what extent this intracapsular development is carried on in the species of *Fusus* and *Murex* cited, I have not been able to ascertain, but it is most probably the case that the protoconch stage is far advanced if not completed before the animal becomes free. The size of the initial whorl of the protoconch is then probably to be regarded as an expression of the size of the embryo, its rapidity of growth during the period of formation of the hyaline primitive shell, and the size it has reached before the deposition of the calcareous matter begins. The size of the yolk of the eggs, i. e., the initial food supply may, in turn, be considered as at least a partial factor influencing this rate of growth. The factors advocated by Boettger are thus secondary factors which may or may not determine survival. They may indeed have no significance whatever, for swollen initial whorls are found in *Fusus colus* which lives in from 10 to 20 fathoms and *F. mamoratus* which lives in even shallower water. Among the Volutes, too, which are comparatively shallow water forms, species like *V. musica* have a minute apical whorl while *V. rupestris* Gmelin, probably belonging to a separate line of development, has a large initial whorl. The initial whorl of the shallow water Fulgurs, is much larger than that of many deep water species of other genera.

Aside from the size of the initial whorl of the protoconch, its obliquity to the axis of coiling of the other whorls is a significant feature. This is found in shells with an emargination or canal, that is fusoid shells, and can be traced back to the beginning of this canal. If the initial emargination, however, forms some distance from the umbilicus toward the periphery of the whorl, the later whorls will coil on a different plane from the first, which is often partially embraced by or becomes sunken into the second whorl (Fig. 6). This early rotation of the first whorl, occurring as it does in the capsular period of development, must be due to characters inherent in the embryo — at any rate it is difficult to conceive how it can be a product of environmental influence on the

animal after emergence from the capsule. It is of course possible that this rotation of the axis of the initial whorl may be a result of the rapid increase in size of this whorl since it nearly always accompanies such rapid increase, in which case it is a secondary feature.

I have elsewhere¹ described in detail the protoconchs of *Rhopalithes* and *Clavilithes* from the Calcaire grossier of the Paris Basin, and shown their great distinctiveness, the species classed under *Rhopalithes* having a fusoid protoconch with few riblets, while typical *Clavilithes* has a papillose one of numerous whorls, with other distinctive characters. I also showed that each genus embraced a series of species which in their stages of development paralleled each other and ranged from the round whorled, ribbed and fusiform type through a number of progressive changes, to an extreme old age or phylogerontic condition. I further pointed out that in spite of this remarkably close parallelism, the generic characters remained constant, the protoconchs of the two series remained distinct and *Rhopalithes* was throughout marked by the presence of columellar plaits (not always visible in old shells unless the lip has been broken back) which never occurred in *Clavilithes*. Moreover, the other shell characters are such that any one familiar with these shells can separate the members of the two series almost at a glance and without reference to the protoconch or columellar plaits. In spite of this Cossmann² insists, and Boettger follows him,—that my distinction is based solely on the difference in protoconchs; and that I carry my faith in the essential constancy of the characters of the protoconch and their phyletic value so far, that I have allowed myself to separate into two genera what M. Cossmann, and others who are accustomed to collect and study these shells in their type-localities, consider to be varieties of one species only. This arraignment might be more serious were M. Cossmann and other high authorities on the shells of the Paris Basin accustomed to study their species serially, and to give due attention to the early conch stages. M. Cossmann has recently taken to a recognition of the diverse characters of protoconchs, and in his valuable “*Essais*” has illustrated many of them. Unfortunately these illustrations are extremely crude,—often merely a spiral line—

¹ Phylogeny of *Fusus*, etc.

² Cossmann, *loc. cit.*

and the wonderful detail shown by many protoconchs is wholly unrecognizable. As for the characters of the early whorls, and their progressive changes, M. Cossmann, like most conchologists, either deems them of minor importance or of none at all, and does not grant them the space they deserve in his descriptions. No wonder then that he should be horrified at my audacity in making a new genus, where he sees only a variety. I was well aware that the species separated by me under the genus *Clavellofusus* were classed by French conchologists as varieties of *Clavilithes parisiensis* (which M. Cossmann still insists upon uniting with the British *C. solanderi* under the name *C. deformis* coined by Brander for the young of that or a related species) for I had specimens labelled thus, presumably by M. Cossmann's own hand; yet I found, and continue to find whenever a new specimen of this series comes under my observation, that the section denominated by me *Clavellofusus* with the rank of a genus, is wholly distinct from, and has its own series of mutations parallel to those of *Clavilithes*. Moreover, if Deshayes is to be believed, this series belongs to the *Sables inférieurs*, while *Clavilithes* belongs to the middle Calcaire Grossier (though one species has been recorded from the *Sables moyens*) except the most specialized terminal member of the group *C. scalaris* which is confined to the *Sables moyens* or lower Upper Eocene. All my material has shown, and I believe that a careful and unbiased study of other material will show that the *Clavellofusus* series is distinct from *Clavilithes* of the Calcaire Grossier, that it runs through its own series of modifications, some accelerated or tachygenetic, other retarded or bradygenetic, and that these various mutations¹ are derived from a *Fusus*-like ancestor, possibly a *Fusus* itself, and not from *Clavilithes parisiensis*, — a species appearing much later and belonging to a distinct genetic series. The *Clavilithes* series is also derived from a fusoid ancestor but a very different one from that which gave rise to the *Clavellofusus* series. If M. Cossmann will admit that my *Clavellofusus* series is a distinct series, — no matter what its origin, — and I do not see how he can do otherwise unless he abjures all regard for phyletic principles — I care not whether he joins me in calling it a distinct

¹ I shall throughout use the term mutation in the earlier sense of Waagen.

genus with species each showing a distinct step in progressive development, or whether he makes the whole series a variety of something and calls my species subvarieties. But he cannot make the series a variety of *Clavilithes parisiensis*, any more than he can make the uncle the son of the nephew.

Professor Boettger will probably find it difficult to point out that the difference between the protoconch of *Clavilithes* and that of *Rhopalithes* is due to any difference in physical environment, as the fusoid members of the series, *C. rugosus* and *R. rugoides* occur side by side, the same being true of other members of the same series as well. Moreover, if he agrees with Cossmann, that *Rhopalithes* and *Clavilithes* are generically identical, he will have to show why the series with the *Fusus*-like protoconch has columellar plaits and why these are wanting in the series with a papillose protoconch.

Finally I may again call attention to the fact that I have described in detail the variation in the protoconchs of *Fusus* and that I have readily admitted the possibility of the existence of larger and smaller initial whorls, of an increase or decrease in the number of whorls in the protoconch, and of the variation in the number of riblets on the protoconch. In fact I have illustrated such variations but I am not ready to admit that there is ever a difference of type in the protoconch in what can otherwise be referred to the same genus. I have repeatedly shown, that the so-called species of *Fusus* from the American Eocene strata not only disagree utterly as regards the type of the protoconch with true *Fusus*, but that the young stages as well show much more acceleration than is found in the young of even modern *Fusus*. "*Fusus apicalis*" and "*Fusus houstonensis*" are an exception to this and it is not impossible, that in spite of the remarkable protoconch, these may be more nearly related to true *Fusi*, than is either *Falsifusus meyeri* or *Fulgurofusus quercollis*.

Fusus aciculatus and "*Fusus*" *serratus* occur side by side in the Calcaire Grossier of the Paris Basin, yet the first retains its normal *Fusus* protoconch while the second has a widely different type of protoconch, like that of many *Pleurotomas*. It will be difficult to explain on the hypothesis of any local cause of variation why *F. aciculatus* retains the early *Fusus* whorls, common to all true

Fusus, and always associated with the Fusus protoconch, while "*Fusus serratus*" with a distinct protoconch has whorls more specialized than those of any other true Fusus, even those of the present day. Why do the fusoid shells in which the normal post-embryonic developmental stages of Fusus occur, always have a Fusus protoconch, while those fusoid shells which do not show the true Fusus protoconch do not show the normal ontogenetic stages of true Fusus, if this is not an expression of inheritance, and of more fundamental significance than Cossmann, Boettger, or Giard are willing to admit? It is high time that we cease making generalizations and tracing relationship by a superficial study of shell characters. Such superficial study has deservedly brought the whole subject of conchology into disrepute, so that morphologists have come to look upon shell characters as the least reliable indices of genetic relationships, whereas they are really the most reliable and delicate of such indices, if subjected to a critical study.

ELIMINATION OF EARLY CONCH CHARACTERS BY ACCELERATION.

It not infrequently happens that the protoconch stops abruptly, and the conch begins as abruptly. In fact, it may be said that this is normal for such specialized types as the fusoid shells (Studies I, figs. 1 and 5). In normal primitive types the protoconch characters may be expected to merge by slow degrees into those of the conch. Such is the case even in types specialized along one direction or another. In highly specialized types, however, we often find an abrupt transition from the characters of the protoconch to those of the conch, these latter beginning suddenly with a number of special characters. Thus in *Fusus*, the protoconch ends abruptly with a strong varix, and the conch begins with round whorls, ribs and spirals. Here protoconch and conch have been telescoped, so that the transitional characters undoubtedly possessed by the ancestors of this genus were dropped out. Conditions of this kind exist in a number of types which may or may not be related to *Fusus*. Such relationship of protoconch and conch cannot of course be regarded as indicating consanguinity wherever it occurs, for it is clearly a stage in development, and therefore a condition, which may appear in the specialized terminal

members of any number of divergent genetic series. Conversely, however, the want of such accelerated conditions in members of the same genetic series may well be regarded as sufficient for generic distinction, though this is largely a matter of personal opinion regarding the elasticity of the generic boundaries. Even greater acceleration than this is shown by many genera. Thus certain species of *Semifusus* have dropped out the round-whorled ribbed stage, the conch beginning with the angular stage (Studies I, Fig. 5).

In many cases the early characters appear not to have been wholly dropped, but greatly condensed, so that the protoconch quickly merges into a highly specialized conch, the transitional stages being extremely short and often scarcely recognizable. Then, too, some of the early stages may drop out without the abrupt change seen in *Fusus*, etc. Thus characters which in the phylogeny of the group were developed only at a relatively late period after other characters had come into existence, may in the specialized members of this series appear immediately after the protoconch, the earlier characters being dropped out of the ontogeny. On the other hand, certain persistent characters may be pushed far back into the ontogeny, and appear even in the protoconch stage. This is seen in the riblets of the last whorls of many protoconchs (*Fusus*) and in the appearance of an angulation or carina in others (certain *Murices*, etc.).

Not only is acceleration by condensation and elimination active in the earliest conch stage, but it is often found at a later period, where some shell character, not strongly fixed in the organization, may be eliminated to make room for a later and more prominent one. This condition has already been briefly described for *Fulgur* and *Semifusus* (Studies I, p. 932) and more fully for *Fulgur* in a later paper (Studies II, p. 528). It may be briefly reviewed here.

In both genera, and in the case of *Pugilina* in what are commonly regarded as varieties of the same species, the tubercles are normally developed as a result of the concentration of the ribs upon the shoulder angle. This is characteristic of the earliest Miocene *Fulgurs* as well as the ancestral forms of *Semifusus* and *Pugilina*. With further development the tubercles grade into a keel and this into a smooth rounded and ribless whorl, differing from the

primitive rounded and ribless whorl in the presence of compound spirals. This is the condition of adult *Fulgur maximum* and certain forms of *F. rapum* of the Miocene. In more specialized types a series of spines appears at periodic intervals on the primary spiral which originally marked the angulation of the shell (Fig. 7). These spines at first small, increase in size progressively up to a certain point. They are simple triangular emarginations of the outer lip and often are abruptly abandoned, so that they remain open forward, though in other cases they are closed in front showing a more progressive abandonment of the spine. This diminution of the spine-forming emargination, is generally more rapid than its development. This condition of newly added spines following in the last whorl upon a smoothly rounded or slightly keeled, non-tuberculate whorl is characteristic of *Fulgur tritonis* (Fig. 7), *F. pilosum*, and others where a fraction of one whorl to several whorls without tubercles or spines separate the primitive tuberculate, from the last spinose whorls (Fig. 7). The same is true of varieties of *Semifusus colosseus* and *Pugilina pugilina* of the modern fauna (Fig. 8). Finally in the most specialized types, such as *Fulgur carica*, *eliceans*, etc., and the accelerated varieties of *Pugilina pugilina*, the spines have been crowded back to such an extent that the non-spinose stages have been dropped out. This telescoping has gone so far as to result in partial overlapping of the spinous and tuberculose stages, as a consequence of which the tubercles pass insensibly into the spines. All stages of this telescoping can readily be observed in large collections of the recent species of *Pugilina* cited.

The significance of this telescoping of characters is often not appreciated. That it cuts out ancestral stages and shortens the ontogeny by this elimination is evident, as is also the resulting vitiation of the phylogenetic record in the ontogeny. Moreover such an overlapping of characters destroys their individuality to a certain extent and makes the later appear to be a mere accentuation of the earlier whereas they have a distinct origin. Such telescoping has apparently occurred in a great number of phyletic series. In Eocene Columbarium, for example, the tubercles grade into the spines in the nepionic stage of the shell. In modern *Columbarium pagoda* (Fig. 6) the tubercles and ribs have been pushed

out of the ontogeny altogether so that the angulation of the ribless whorls and the appearance of true spines is almost simultaneous. Yet the Eocene species indicate that the genus passed through a normal series of round-whorled-ribbed, and angular-whorled-tuberculated stages before the spines appeared. As already noted, a second row of spines appears in several lines of radiation in this series. In the genus *Rhinocanthus*, typified by *Murex* (*Rhinocanthus*) *brandaris*, the principal spine likewise merges with the tubercles which here are formed without the loss of the ribs. The second spine has also been accelerated until it appears during or shortly after the tubercled stage. In the more specialized Murices, where the adult spines are compound, the early ones have been pushed far back and are inseparable from the tubercles or even from the ribs. It seems in fact that the spine-forming stage has become superposed upon the rib-forming stage for the ribs are characteristic of adult Murices of such relatively simple types as *M. brandaris* and of such highly complicated types as *M. palmarosae* as well.

In tracing the phylogeny of spinous gastropods it must be borne in mind that tubercles and spines have a different origin, and that where they appear to merge into each other this is due to acceleration. It is highly probable that the ancestral forms of such types will be found to have these two characters separated, the spines not being found in the earlier members of the phyletic series as has been demonstrated to be the case in *Fulgur*.

As has been shown above, the ontogeny of a great many widely distinct types of gastropods is marked by a progressive increase in the amount of embracing of the earlier by the later whorls. This results in a change of angle of the spire from relatively acute in young to often a rectangle or obtuse in the adult. In some types (*Conus*) the change may be to 180 degrees, rarely more. This same change is observable in the adults of the successive members of the corresponding phyletic series. Thus the Eocene species of *Fusus* are characterized by a slender spire throughout, while the modern forms usually show the slender spire only in the youthful stages, the adults becoming more broadly turreted. In *Tudicula*, the Miocene species show a more slender spire, especially in the young, than is shown in the modern species. A similar

condition is observable in *Turritella*, where the early species are generally more loosely coiled. Such looser coiling is also observable in the young of modern forms, in the adult of which the whorls embrace up to the angulation. Here however another factor enters in, the progressive flattening of the whorls so that the spire remains slender even though the whorls embrace to the ambitus. Similar conditions obtain in *Nerinea*, *Cerithium*, and others, the surface of the whorls even becoming concave in many of these.

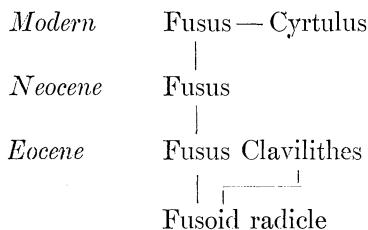
In its most pronounced form the progressive increase in the amount of embracing of the whorls is seen in phylogerontic types. Here this increase is accompanied by a loss of ornamentation and distinctive form. In its most striking form this excessive embracing is seen in *Melongena*, where the earlier whorls become to some extent enwrapped by the later ones, the form of these later whorls bearing no relation to that of the earlier ones, but being without the normal ornamentation of the earlier whorls (Studies I, fig. 9). Similar though more regular conditions are found in the clavilithoids for a discussion of which the reader is referred to my "Phylogeny of *Fusus*." Cossmann has recently reiterated his belief in the generic relationship of *Clavilithes* and *Cyrtulus* which latter type is a phylogerontic terminal of the modern *Fusus* series. This reassertion of his former position indicates that Cossmann has either not carefully read my arguments for the total distinctness in origin of these types — or if he did, that he does not consider them as valid. If this is the case I must give up all hope of convincing him, for I do not see that I can state the case more fully. If any one not biased by inherited ideas of relationship indicated by adult characters, will carefully compare the young of *Cyrtulus serotinus* Hinds with the nepionic and neanic stages of any species of *Fusus* of the *F. colus* series, he will be impressed with the similarity of these two types, a similarity which so far as the details shown are concerned, amounts to identity. I do not believe that any one can distinguish the young of *Cyrtulus serotinus* from that of any member of the *Fusus* series, unless he finds some characters not yet observed in these types. Certain it is, that the young of this species, is more nearly identical with that of any member of the *Fusus colus* series than with any other known gastropod. This similarity can only be the result of relationship, so that the unbiased

investigator will probably be forced to accept this evidence as indicative of community of descent. If we now take the most closely similar type of the Eocene clavilithoids, which I think all will agree is found in the forms I have classed as *Clavellofusus* — but which Cossmann still considers varieties of *Clavilithes parisiensis* Mayer-Eymer (*Clavella deformis* of Cossmann) we find that its young leads us to some Eocene or earlier fusoid ancestor which may or may not have been the ancestor of the modern *Fusus*, including the *Fusus colus* series as well. Assuming, for the sake of making the argument as favorable as possible to M. Cossmann, that *Fusus* and *Clavilithes* had a common ancestor,— which, moreover, is probably the case — and allowing for the moment that my species of *Clavellofusus* are varieties of *Clavilithes parisiensis* as Cossmann contends,— but which most certainly is not the case — if we allow this, where do we land? In the first place, if youthful characters show relationships at all,— and I doubt if in view of all the evidence accumulated along so many and diverse lines, even Cossmann will have the hardihood to deny this — it is evident that all the Eocene clavilithoids are derived from an Eocene or earlier fusoid ancestor, which we will allow was a true *Fusus* and the ancestor of the modern *Fusus* as well. Nevertheless, it remains true that *Cyrtulus serotinus* is a derivation of modern *Fusus* and not of Eocene *Fusus*, a point established beyond question by the character of its young.

If Cossmann were to contend that both the modern and the Eocene clavilithoids were derived directly from a common Eocene or earlier ancestor there would be some reason in his gathering all these divergent lines into a common generic boundary. The question would then be boiled down to that of the greater or less elasticity of the generic boundaries. But Cossmann holds that *Cyrtulus serotinus* is a descendant of *Clavilithes* (“quoiq’elle [*Cyrtulus*] soit le descendant immédiat des *Clavilithes*”) although the young stages show that this is not the case, as every student of phylogeny of Mollusca as deduced from shell structure will readily admit on comparison. Unless, then, Cossmann can prove the direct derivation of *Cyrtulus serotinus* Hinds and *Clavilithes*

¹ loc. cit. 1904, p. 234.

parisiensis Mayer-Eymar (or better *Clavellofusius spiratus*) from a common Eocene or earlier ancestor, without the intermediation, in the Cyrtulus line, of modern Fusus, his proceeding would be almost as illogical as the classification of all ammonoids showing a corresponding degree of involution in the same genus. This will appear more clearly from a consideration of the following diagram.



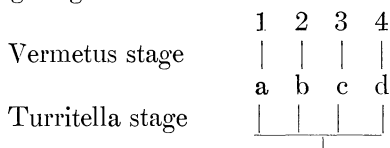
The only other way, in which Clavilithes and Cyrtulus can be made congeneric, is by also including Fusus in this genus, a stretching of generic limits, to which even M. Cossmann will most certainly object.

I have elsewhere¹ outlined in detail a number of genetic series among the Clavilithoids which, diverging probably from a common ancestor, produced similar end forms, just as divergent ammonite phyla often had end forms superficially alike. Whether the series which I have outlined to the degree of detail permitted by the available material, will be found to be complete, or will need modification in the future, remains to be seen. That the various series exist, is, I think, beyond cavil, and certainly cannot be set aside by a wholesale assertion of authority even on the part of the most veteran collector of these fossils.

It has already been outlined in the earlier part of this paper, that old age characters in gastropod shells are also shown by the loss of the power to coil, as is so commonly the case in cephalopods. That such characters have been taken as distinctive of new genera is not surprising, and indeed is desirable. Great caution however is necessary not to make this the sole distinguishing character, and class together terminal loose-coiling members of distinct genetic

¹ Phylogeny of Fusus. Smithsonian Miscellaneous Collections, vol. XLIV, no. 1417, 1904.

series. That this has been done in *Vermetus*, admits of little doubt. The Mesozoic and Tertiary species of this group represent phylogerontic terminals of various genetic lines of turritelloids, becoming extinct in these periods, just as modern species represent terminals of one or more lines of modern turritelloids. Even if the species of turritelloids are considered as congeneric throughout, the terminal vermetoids cannot be congeneric but merely represent a stage in development. Each terminal group would of necessity represent a distinct genus unless it were united in one genus with its corresponding ancestral turritelloid, as in the following diagram.



Thus if *a*, *b*, *c*, and *d* represent four diverging specific lines of *Turritella* and 1, 2, 3, and 4 the corresponding *Vermetus* form, these latter could not be classed as one genus, *Vermetus*, unless *a*, *b*, *c*, and *d* were also classed in the same genus. Each must be considered as a separate genus whether it has one or more species, but 1 and *a*, 2 and *b*, 3 and *c*, 4 and *d*, can each be classed as a distinct genus, with a turritelloid and a vermetoid species, or all species of vermetoids may be classed as *Turritella*.

This reasoning applies with equal force to the non-coiling forms commonly classed as *Platyceras*, this term having the value of a stage. A similar though very slight loosening of the last whorl is made the basis for the separation of the genus *Diastoma* from *Melania*, although pathologic individuals of the latter sometimes show an identical character (Fig. 19). That in the case of this so-called genus we really deal with a stage in development, and therefore with terminal members of different phyletic series, which ought to be united with their respective *Melania* ancestors instead of being classed together, becomes more apparent as the detailed study of these types progresses.

In extremely accelerated series it often happens that the mode of development appears to be reversed, the specialized character appearing first, and the less specialized later. Thus in certain

Melantias in *Cerithium*, *Turritella*, etc., ornamentations appear in the young which are lost in the adult. Without departing from an orthogenetic mode of development, the succession of characters developed seems to be inverted. In such cases it generally appears on study of the youngest stages that the simple characters of the adult are similar to the most youthful characters, before the most pronounced features appear. This feature will be described later in some detail in certain Melantias and is also seen in other specialized types. It is readily explained by referring it to degradational development, where characters acquired during the aggradational period are lost in the reverse order of their acquisition. Sometimes differential acceleration may account in part for this. Thus in some cases, the shell becomes carinate and only subsequently develops ribs. These may be a later acquisition having never before appeared in the phylogeny of this series. Whatever the cause of such development, the method is orthogenetic, the variation being in all cases progressive in one direction or another.

EXAMPLES ILLUSTRATING ORTHOGENESIS.

I have elsewhere described a considerable number of genetic series among the fusoid shells¹ and have also traced in some detail the development of the *Fulgur* and *Sycotopus* series (Studies II). It has there been clearly shown that the development is orthogenetic, both as regards phylogeny and ontogeny, and that the great governing principle in the production of diversity is acceleration or tachygenesis, and retardation or bradygenesis. To show more clearly the universality of this principle of orthogenetic variation among the Gastropoda, I will here append a somewhat detailed discussion of several phyletic lines among the Melantias, a group as distinct as possible from the Fusidae. Unfortunately in the specimens studied, the protoconchs were not available, so that all the deductions are based upon the characters of the conch, from its earliest to its latest stages.

Melania is well adapted to this sort of study on account not only of its variability, but also because it has so many characters upon

¹ loc. cit.

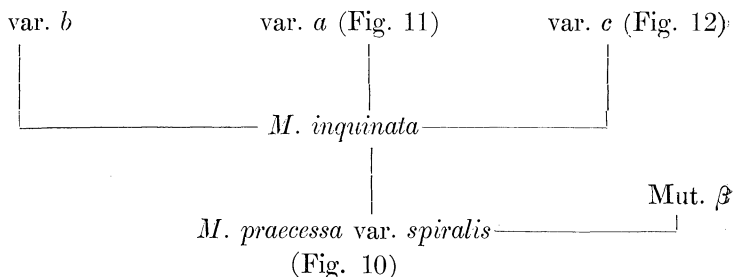
which we can seize for the purpose of determining the line of progress. The earliest types were undoubtedly marine giving rise on the one hand to the fresh water *Melantias* and on the other hand to a number of marine descendants. No exhaustive discussion is contemplated here, this and the tracing of the various genetic lines being reserved for a future work. Only some of the more salient features developed during the study of this group of shells will be mentioned here as illustration of the principles discussed.

The Eocene *Melanoides praecessa* and *M. inquina* of the Paris basin may be taken as a starting point, though they already present characters of considerable complexity both showing a marked series of changes. In the former the earliest stages observed show rather flatly rounded whorls with distinct, narrow, rounded ribs which are concave forward (i. e., towards the aperture). These ribs are cancellated by revolving spirals which however are faint in the interspaces, but form pronounced nodules on the ribs. In some specimens the earliest ribs appear to be free from these tubercles, and the mode of appearance seems to indicate that the ribs precede the spirals. This is the character of the early stages of the type specimen figured and described by Deshayes (Des., An. sans. vert., II, p. 452, pl. 23, figs. 31-32) these stages being free from spirals. This character recalls the adult of *Pseudomelania* (*Chemnitzia*) *undulata* d'Orb., *Ch. carusensis* d'Orb., *Ch. corvaliana* and *Ch. periniiana* d'Orb., from the Middle Lias and *Ch. rhodani* of the Upper Lias of France.¹ In later Jurassic strata of France occur many *Pseudomelantias*, which show no ribs in the adult. Some of these may however possess them in the young, as has actually been found in the case of *P. nereis* d'Orb. of the Bathonian. Such occurrences suggest that the smooth *Pseudomelantias* are derived from the ribbed ones and hence in so far as they have lost this character are phylogerontic.

In Eocene *Melanoides praecessa* var. *spiralis* var. nov. from Noyon (C. U. coll. 30041, fig. 10) the spirals become gradually strengthened, until they are well marked. The uppermost or posterior spiral becomes strongest; and gradually the space above it develops into a concave shoulder free from ribs. On this shoulder-

¹ D'Orbigny. Paleontologie Francaise.

angle develops a series of nodular spines, as the ribs gradually become obsolete, slightly fainter nodules being formed where the lower spirals and ribs cross. With the complete disappearance of the ribs, the lower spirals—of which there are four large and three smaller more closely crowded ones in the adult—become continuous and free from nodulations. No intercalated or secondary spirals occur, except in accelerated types, where the shoulder and nodules exist for only a few neanic whorls, after which they gradually disappear, only faint primary and secondary spirals remaining on the last whorl (Mut. β Fig. 9; C. U. coll. 30042). In the type specimen of *M. praecessa* figured by Deshayes, the ribs have not entirely disappeared in the adult. It represents a more primitive or more retarded individual than the Noyon variety described above, its adult features being comparable to the early neanic of var. *spiralis* Grabau. Three varieties of *M. inquinata* (Def.) are figured by Deshayes (Coq. foss. Em. Paris II pl. 12), of these var. *a* (Desh., figs. 3 and 14, our fig. 11) is the immediate successor of *M. praecessa* var. *spiralis*, but the tubercled character, which in that variety occurs only in the adult, is here found in the neanic and perhaps even in the nepionic whorls. Var. *b* (Desh., figs. 15, 16) is characterized by the suppression in the adult of all the spirals except the one on the angle, on which the tubercles become greatly strengthened, and the spiral just above the suture which is non-tuberculate. Both shoulder and body of the whorls become strongly concave in the adult. The third variety (*c*, figs. 7 and 8 of Deshayes) has all the tubercles suppressed, while the spirals become strong and the whorls below the shoulder rounded (Fig. 12). The phyletic relationships of these types may be expressed as follows, the length of line representing relative amount of divergence.



M. praecessa var. *spiralis**M. praecessa*

(Desh., An. sans Vert., II, pl. 23, figs. 31-32)

Jurassic ribbed *Pseudomelania*

(D'Orbigny, Pal. Francaise)

An interesting line of departure is shown in some specimens of *M. praecessa* var. *spiralis*. Here the second spiral from the posterior suture is the strong or primary one; *i. e.*, early in the ontogeny a new spiral appears above (posterior to) the primary one. This continues on the shoulder, and before the disappearance of the ribs becomes somewhat tuberculose. Intercalated spirals also appear on the adult whorl. This appears to have been the lineal ancestor of *Melania asperata* Lam. var. β Brot, of the Philippine Islands, a fresh water type (Figs. 14 and 15). The less accelerated individuals of this form show the early ribbed whorls, though these are marked by a large number of closely set extremely fine spirals not observed in the Tertiary species. In the individual represented by Fig. 15, a single row of spines makes its appearance after five or six volutions. These spines appear near the center of the exposed whorl, one on each rib, and begin shortly before the appearance of the ribs themselves (Fig. 17). At first the spines are very weak but gradually they increase in size, at the same time beginning earlier and ending abruptly upon the rib. Together the spines and their posterior prolongations produce the appearance of spirals. The single row of spines continues for almost four volutions the whorls gradually becoming divided into shoulder and body with the spines on the pronounced shoulder angle. A second row appears on the shoulder beginning as a faint elevation which is gradually strengthened.

In a more accelerated individual (Figs. 14 and 16), the second row of spines appears almost simultaneously with the first one though the lower row becomes somewhat more strongly accentuated.

Strong spirals appear on the body of the whorl without the formation of spines, one or sometimes two of these spirals appearing above the suture of the succeeding whorl. Intercalated spirals occur on the body of the last body-whorl.¹

These *Melantias* therefore seem to be extremely accelerated, the spines appearing while the ribs are still in full force.

A type apparently retarded as far as the form is concerned is found in *M. dactylus* Lea from the Philippines (Martini Chemnitz *Melania* pl. 9, figs. 2 and 2a) in which two whorls of the adult are marked by narrow crescentic ribs cancellated by numerous spirals which appear in the earliest part of the ribbed whorls. The initial whorl is not known but the whorls immediately succeeding are smooth in appearance and embrace to the ambitus. Whether or not fine spirals occur on the earliest whorls is not ascertainable. The succeeding whorls embrace less, thus producing the slender spire. In the adult of many individuals the ribs become obsolete that being the usual line of development. Brot (Martini Chemnitz I 24, pl. 9, fig. 2a) however figures a specimen which successively acquires two rows of tubercles in the adult thus paralleling *M. asperata* var. β of the Philippines.

While these types show aggradational progression, modified by differential acceleration and retardation, other species referred to *Melania* show degradational progression, i. e., a progressive modification through suppression of characters. Certain Jurassic *Pseudomelantias* showing this have already been mentioned. A modern example is *Melania elevata* Say from Indiana. Here the late nepionic and neanic whorls are carinated, this carina gradually disappearing the shell becoming smooth and with scarcely impressed suture and with spirals only on the lower part of the whorl. The aspect is that of *Pseudomelania*, the character being derived through progressive reduction of features inherited from specialized ancestors.

The same thing is true of *M. deshaysiana* Lea, and *M. costulata* Lea from Tennessee. Here the order of development seems to be entirely inverted, the earliest whorls being carinated while the later ones show successive suppression of the carina, and the

¹ See Martini und Chemnitz, Syst. Conch. Cab. I 24 pl. 8, figs. 1, 1b and 1f.

strengthening of the ribs and spirals until in the spiral whorl the ribs and spirals gradually disappear. So far as shown by the specimens examined, which all lack the apical whorls, the ribs are absent from the early carinate whorls. It is possible that the carinate whorls are preceded by rounded ribbed whorls but of this we have at present no evidence. Should this eventually prove not to be the case, the explanation of these characters must be found in the early acceleration of the carina, which appeared on the smooth whorls before the ribs had appeared these latter not coming in until the time of disappearance of the carina. In *M. strigosa* Lea from the same locality, ribs seem to be wanting altogether, the early angular whorls passing by disappearance of the keel and spirals into a smooth adult form. Other species having smooth adult, and ribbed and spiralled youthful form are *M. rustica* Moussen (Martini Chemnitz pl. 17; 2 a, b), *M. palimpsestos* Reeve (Martini Chemnitz pl. 17; 3), and *M. hastula* Lea (Martini Chemnitz pl. 16; 3, a-d).

Claviger subauritus Brot represents the more primitive condition of that genus, in which the whorls are ribbed, the single row of tubercles being developed only on the last whorl (see Martini-Chemnitz I 24, pl. 36, fig. 11a).

The extremely spinose types of Melanias such as *Claviger byronensis* Gray (Martini Chemnitz pl. 36; 10a-c), and *C. auritus* Müller (Martini Chemnitz pl. 36; 7a-c), represent accentuations of one character at the expense of the others,—a one-sided acceleration. In the latter species the nepionic whorls show ribs and spirals the central of which become fused with two adjoining ones. This fused series quickly becomes accentuated in a pronounced tubercle, which increases in size and becomes variously modified while the remaining portion of the shell becomes smooth. At first the tubercles are near the middle of the whorl but gradually as they increase, the relative amount of embracing increases until the tubercles of the adult whorl lie just above the suture. In *C. byronensis* two groups of spirals become tuberculated, a third one occurring in some varieties.

A closely parallel series of variations is found in the modern *Potamides fuscatus* of Gambia. The nepionic and early neanic stages are identical with the adult of *P. granulatus* (Brug.) (*P.*

corvenii Fer.) of the same locality. This begins with a round-whorled ribbed stage passing into an angulated stage in which the spirals are prominent. The ribs progressively break up into tubercles, those on the median spiral being more prominent. In accelerated individuals (*P. radula* Linn.) the upper of the two median spirals has its tubercles slightly more accentuated than the lower, while a secondary spiral between them is also slightly tuberculated. The young of *P. fuscatus* Linn. shows the bicarinate whorls, the spirals forming the two carinae being tubercled. Somewhat later the upper series of tubercles becomes accentuated and a secondary spiral appears between the two. Up to this point, perhaps one fourth the length of the shell or less, all the stages except the earliest of *P. granulatus* are repeated, so that the young of *P. fuscatus* is in effect a diminutive *P. granulatus*. The further development of *P. fuscatus* is along the line of accentuation of the tubercles of the upper spiral, until they have become pronounced, sharp, and spine-like in the adult, all the other spirals, except the one just above the suture, disappearing in the most specialized examples. The series in this case is as complete as is that of the spinose Clavigers, and representative species, showing the same stage of development so far as the surface characters are concerned can be selected in both series.

The carinated Melanias represented by *Claviger matoni* Gray (Martini Chemnitz pl. 37; 3, 3a-f; 4, 4a-b) from Senegal show another interesting type of modification. The primitive species (*C. mutans* Gould, Martini Chemnitz pl. 37; 3b-e) are spiralled and ribbed, the upper spiral being the stronger. In somewhat more accelerated individuals the ribs are lost on the last whorl, but the spirals continue and become stronger, especially the upper one which begins to extend outward as a strong flange forming a deep notch or sinus in the lip. Somewhat more accelerated specimens show two or three final whorls in this condition, the flange of the last one becoming extremely pronounced, while one or in case of more loosely coiling individuals, two of the lower spirals also begin to be strengthened. Finally in extremely accelerated specimens, the ribbed and spiraled portion is restricted to the apical part, and it passes almost abruptly into a smooth shell on which the upper spiral makes a pronounced flange-like carina,

while the one just above the suture also becomes very pronounced. Sometimes this latter is prevented from taking part in the ornamentation of the shell by the close coiling of the whorls, the succeeding whorls crossing this spiral. (Martini Chemnitz, I 24, pl. 37, fig. 3-3a). Differentially accelerated specimens may have the flange pushed back into the ribbed portion; i. e. the flange appears before the ribs disappear. Then the flange is broken up into blunt vertically flattened spines which unite into a keel as soon as the ribs disappear entirely.

We have thus in the *Melantias*, a group of highly accelerated gastropods in which the spines,—a specialized feature, appearing late in the phylogeny of most gastropods—have become a dominant character, appearing before the ribs have disappeared. Many phylogerontic members of this group, forming terminals of genetic series, retain their ornamentation only in the young, the adults becoming smooth. In several lines extreme accentuation of certain characters at the expense of others has resulted in grotesque forms. All the characters, however, appear and disappear in a regular progressive manner both in ontogeny or individual development, and in phylogeny or the development of the genetic series. The *Melantias* therefore constitute an excellent group from which illustrations of ortho-ontogenesis and ortho-phylogenesis may be obtained.

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PLATE I.

FIG. 1.—*Tudicula bispinosa* Grabau; young individual, showing beginnings of second row of spines. (Col. Univ. Coll. 30045.)

FIG. 2.—*Tudicula rusticula* (Basterot); early stages enlarged $\times 10$, to show looser coiling and gradual appearance of spines and angulation. (C. U. Coll. 30046.)

FIG. 3.—*Tudicula bispinosa* Grabau; a somewhat older individual than that shown by fig. 1. (C. U. Coll. 30047.)

FIG. 4.—*Tudicula bispinosa* Grabau; showing two rows of spines fully developed (C. U. Coll. 30048.)

FIG. 5.—*Tudicula rusticula* (Basterot); a characteristic adult form with a single row of spines.

All the above are from the Miocene. Fahluns de Bordeaux.

FIG. 6.—*Columbarium pagoda* (Less.) Recent protoconch and early conch stages enlarged $\times 10$, showing elimination of ribbed ancestral stages. (C. U. Coll. 39782.)

FIG. 7.—*Fulgur tritonis* Conrad. Summit view of a characteristic specimen, showing the smooth neanic stage and the gradual development of the spines. (C. U. Coll. 30052.)

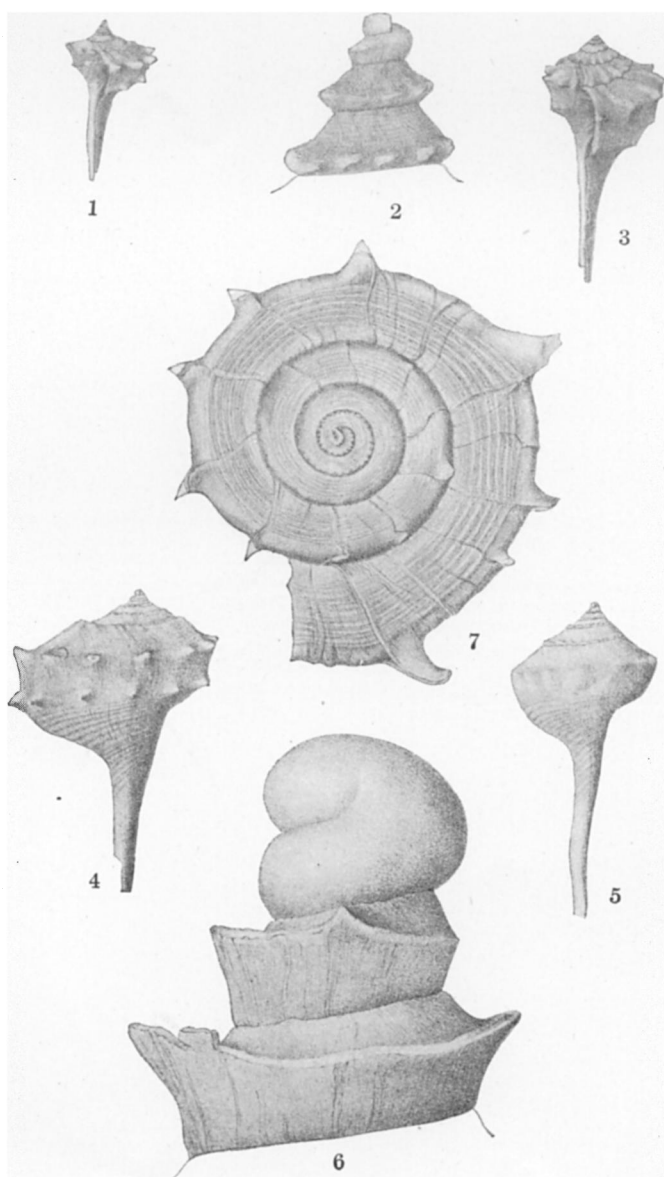


PLATE 2.

FIG. 8.—*Pugilina pugilina* (Born); a primitive mutation retaining the smooth stage in the neanic. (C. U. Coll. 39818a.)

FIG. 9.—*Melanoides praecessa* var. *spiralis* Grabau Mut. β ; showing disappearance of nodules in later stages. Lower Eocene, Noyon. (C. U. Coll. 30042.)

FIG. 10.—*Melanoides praecessa* var. *spiralis* Grabau. Type. Lower Eocene, Noyon. (C. U. Coll. 30041.)

FIG. 11.—*Melanoides inquinata* (Def.) var. *a* Desh.—Copy of Deshayes figure.

FIG. 12.—*Melanoides inquinata* (Def.) var. *c* Desh.—Copy of Deshayes figure.

FIG. 13. *Melania* sp. An unidentified species from the Tertiary of Abyssinia showing appearance of second and later spirals, partly by intercalation. Much enlarged. (C. U. Coll. 30054.)

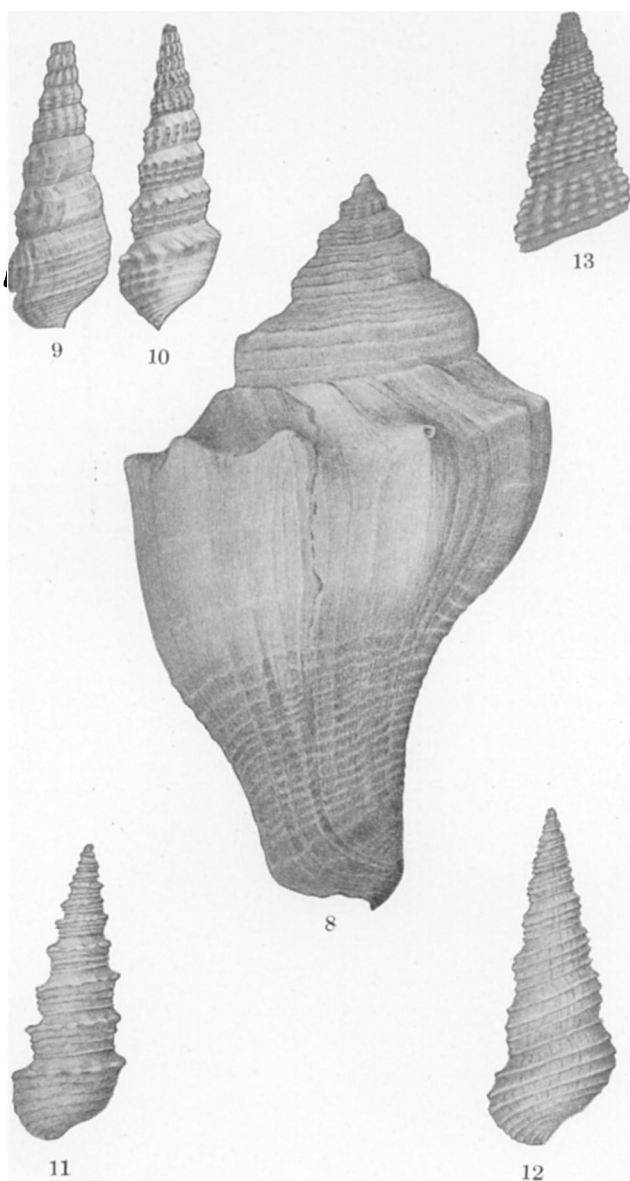
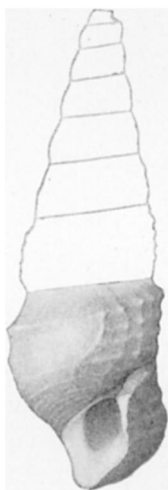


PLATE 3.

- FIG. 14.—*Melania asperata* Lam. var. β Brot. Recent, Philippines. Accelerated mutation with two rows of spines appearing almost simultaneously. (See fig. 16.) (C. U. Coll. 41517.)
- FIG. 15.—*Melania asperata* Lam. var. β Brot. Recent, Philippines. A mutation with a single row of spines in the young. (See fig. 17.) (C. U. Coll. 41518.)
- FIG. 16.—*Melania asperata* Lam. var. β Brot. Enlargement of young stages of fig. 14.
- FIG. 17.—*Melania asperata* Lam. var. β Brot. Enlargement of early stages of fig. 17.
- FIG. 18.—*Melania* sp. An unidentified species from the Tertiary of Abyssinia showing appearance of third spiral by intercalation. Much enlarged. (C. U. Coll. 30053.)
- FIG. 19.—*Melanoides praecessa* var. *spiralis* Grabau. A senile individual showing loosening of last portion of whorl, a feature regarded as characteristic of *Diastoma*. Enlarged $\times 2$. Eocene, Bordeaux. (C. U. Coll. 30043.)



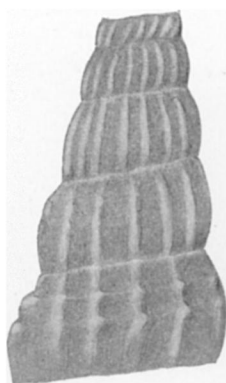
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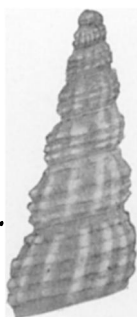
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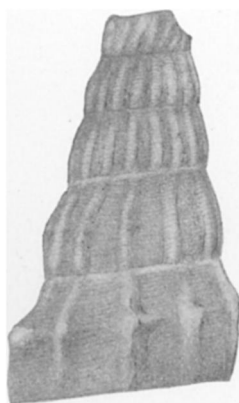
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